

AN ECOLOGICAL STUDY OF BRISTLECONE PINE (*PINUS LONGAEVA*) IN UTAH AND EASTERN NEVADA¹

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ABSTRACT.— This paper presents data on the distribution of *Pinus longaeva* on the Markagunt Plateau, Utah; and the Snake, Egan, and White Pine ranges of eastern Nevada. It also presents data on the present-day density and age structure of three *P. longaeva* populations and the growth rates of individual trees within these populations.

Conifer species richness and the relative abundance of *P. longaeva* varies clinally from the Markagunt Plateau to the White Pine Range. The Markagunt Plateau has relatively high conifer species richness (10 species) and low relative abundance of *P. longaeva* (1%). The White Pine Range has low conifer richness (4 species) and high *P. longaeva* relative abundance (34%). Individual tree growth rates were low but highly variable in all populations studied. The three populations studied had mixed age structures with a general trend of more younger individuals at the lower elevations.

Possible explanations for the present distribution of *P. longaeva* and the population structures observed are discussed.

The distribution and abundance of a species results from the interaction of several environmental parameters. Innate factors such as nutrient and moisture requirements, vegetative growth rate, and age to first reproduction interact with and are influenced by physical and biotic factors of the environment. If the ecology of a species is to be understood, the relative influence of these and other parameters on its distribution and abundance must be determined. Without this information, predictions about the future health and dynamics of populations cannot be made. Such predictions are especially difficult for long-lived species whose population dynamics cannot be followed over time. For such species present-day characteristics of its population such as density, age structure, and individual growth rate must be used to describe past fluctuations in population size, to evaluate the present status of the population, and to predict future growth or reduction in population numbers. Such analyses may be especially valuable in devising management plans for rare or endangered species.

This paper represents a study of the ecology of four bristlecone pine (*Pinus longaeva*) populations located on selected mountain

ranges in Utah and Nevada. It describes the distribution of bristlecone pine in western Utah and eastern Nevada and attempts to document, by use of present-day densities, age structure, individual growth rates, and spatial and temporal fluctuations within these stands. *Pinus longaeva* was selected for study due to its great longevity, its interesting biogeographical distribution, and the existence of relatively undisturbed stands.

SPECIES DESCRIPTION.

Based on morphological considerations, Bailey (1970) split bristlecone pine into two species. The Colorado and New Mexico populations retained the name *Pinus aristata* Engelm., and populations west of the Colorado River were designated *Pinus longaeva* Bailey (Bailey 1970). Subsequent studies of the terpenoid chemistry and crossability of the two forms provided further support for two species (Mastroguiseppe 1976, Zavarin et al. 1973, 1976, Critchfield 1977). The latter species, *Pinus longaeva*, is the subject of this study.

Pinus longaeva is generally found at high altitudes, often extending to timberline on

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the mountain ranges of Utah and Nevada and the White Mountains of eastern California. It is typically localized in areas with poor soils but may also form extensive stands. Isolated trees can be found on mesic sites with sufficient sunlight (Wright and Mooney 1965, Beasley 1980). On these sites, *P. longaeva* has a fast-growing, erect growth form instead of the twisted, gnarled, slow-growing form that predominates on poor sites. It has also been observed to form krumholtz at its upper elevational limits. One of the best known and most interesting characteristics of *P. longaeva* is its great longevity, as it attains ages approaching 5,000 years (Currey 1968, Ferguson 1968).

The present distribution of *P. longaeva* in the Great Basin is on isolated mountain ranges separated by xeric valleys of sagebrush and shadscale. At the higher elevations the environment of these ranges is more favorable, with some ranges supporting diverse communities of montane conifers. The most eastern ranges are generally more mesic since precipitation in the Great Basin decreases to the west. Perhaps as a result, the number of conifer species decreases from 10 on the eastern ranges to as few as 2 on the most western ranges (Critchfield and Little 1966). Associated with the decrease in conifer species richness is an increase in the relative abundance, size of stands, and altitudinal range of bristlecone pine.

We are aware of no studies of the population ecology of *P. longaeva*. Previous studies of bristlecone pine have been concerned with the establishment of paleoclimatic records through the use of dendrochronology techniques (Ferguson 1970c, Fritts 1965, LaMarche et al. 1974, Wilson and Grinstead 1975) and with the ecological physiology of this species. Eco-physiological studies have generally focused on finding explanations for its tolerance to extreme habitats and great longevity (Schulman 1954, Fritts 1965, LaMarche 1969, Mooney et al. 1966, Schultze et al. 1967, Wright et al. 1965, Beasley et al. 1971). Recently we (Hiebert and Hamrick 1983) published genetic data that was consistent with what is known of the recent paleoecological history of *P. longaeva* in the

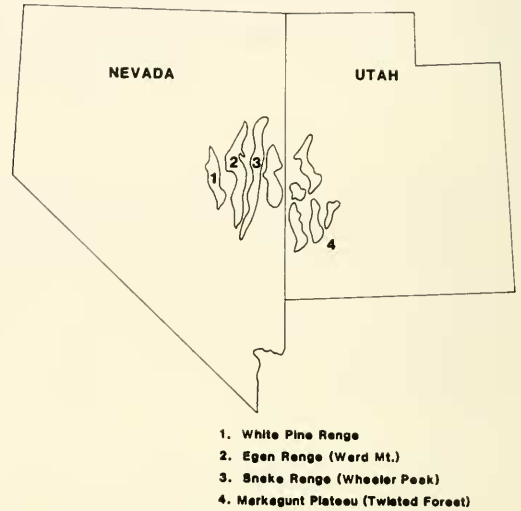


Fig. 1. Locations of mountain ranges and *Pinus longaeva* populations included in this study.

Great Basin (Wells 1983). We observed high genetic variations within populations and low genetic variation between populations. Paleoecological studies have shown bristlecone pine to form large contiguous populations throughout much of the Great Basin during glacial episodes during the last 40,000 years.

STUDY SITES

The population ecology of *P. longaeva* was investigated on four mountain ranges in Utah and eastern Nevada. The ranges included from east to west the Markagunt Plateau (north rim of Cedar Breaks) in Utah, and the Snake, Egan, and White Pine ranges of eastern Nevada. Three populations were selected for more detailed ecological studies: Twisted Forest (TF), Markagunt Plateau; Wheeler Peak (WP), Snake Range; and Ward Mountain (WM), Egan Range (Fig. 1). Twisted Forest and Ward Mountain stands occur on limestone substrate, and the Wheeler Peak population is on quartzite glacial till. The population at Wheeler Peak is located on a west- to northwest-facing slope at an elevation of 3250–3500 m. The other two populations range between 2700 and 3200 meters in elevation. Most of the population at

Twisted Forest is a monospecific stand of *P. longaeva*. The understory is completely bare except for a dwarfed *Castilleja* (Indian paintbrush) species. However, at the lower boundary of the population (a stream bed), bristlecone pine is associated with *Pinus flexilis*, *Picea engelmannii*, and *Pseudotsuga menziesii*. In the Wheeler Peak population, bristlecone pine shares dominance with *P. engelmannii* and *P. flexilis*. The lower edge of the population drops into a mesic canyon, where vegetation is dominated by a dense stand of *P. engelmannii*. On Ward Mountain, bristlecone pine is associated with *P. engelmannii* on north-facing slopes and with *P. flexilis* on the more open, exposed sites. The understory there is dominated by *Artemisia tridentata*.

METHODS

Montane and subalpine conifer species richness, relative abundance, and dispersion were obtained for each mountain range by establishing altitudinal transects extending along equivalent compass points from the highest peak or timberline to the lower boundary of the montane conifer zone. Every tree within 5 m of the transect was tallied, and observations were made on the topography and soils of those habitats where bristlecone pine occurred.

To estimate population parameters for the three bristlecone pine stands, two or three vertical line transects and two horizontal line transects were subjectively chosen. The point-quarter method of Cottam and Curtis (1956) was employed to sample bristlecone pine at 100–150 m intervals. The sample consisted of 24 points/population. Sample trees were tagged, DBH measured, height estimated, and one radial core was taken at breast height (4½ feet) using a 40-cm increment core. The cores were mounted on grooved boards in the field and returned to the laboratory for counting.

Increment cores were polished, and the number of growth rings along one radius was counted using a binocular microscope. Due to short growing seasons at high altitudes, there was little difficulty with false growth rings. When a complete core to the center of

a tree was obtained, the number of rings was assumed to represent the minimum age of the tree. For trees with incomplete radial cores, total age was estimated. Trees of known age and diameter were used to estimate ages of trees with incomplete cores for which actual tree average growth rates and diameters were known. Growth rates of the individual trees gave the best estimate of age, with correlation coefficients ranging from 0.89 to 0.95 for the three populations. The accuracy of this prediction was best for large trees whose ages we were most interested in estimating. Thus, for trees with incomplete radial cores, a core of 40 cm was obtained, the rings counted, and the average growth rate determined. The average growth rate of the tree was then used to estimate the number of growth rings in the uncored radius.

Population densities were calculated using standard point-quarter techniques (Cottam and Curtis 1956). The average increase in DBH/year was determined by dividing the diameters of the trees by their age.

Size structure of the populations was determined by calculating the frequency of trees within 20-cm diameter classes. Age classes were set at 250-yr intervals.

Mean ages were also calculated and the Student-t-test applied to determine whether significant differences occurred among populations, or among different areas within populations.

RESULTS

Montane and subalpine conifer species richness and the relative abundance of *P. longaeva* varies clinally from the Markagunt Plateau to the White Pine Rangé (Table 1). Montane and subalpine conifer species richness is relatively high on the Markagunt Plateau (10 species) and the Snake range (8 species) but is lower on the more western Egan and White Pine ranges (5 and 4 species). Associated with the decrease in conifer species diversity from east to west is an increase in the relative abundance and altitudinal range of *P. longaeva* (Fig. 2). *Pinus longaeva* is usually restricted to poor edaphic conditions on the Markagunt Plateau and the Snake Range and has correspondingly abrupt

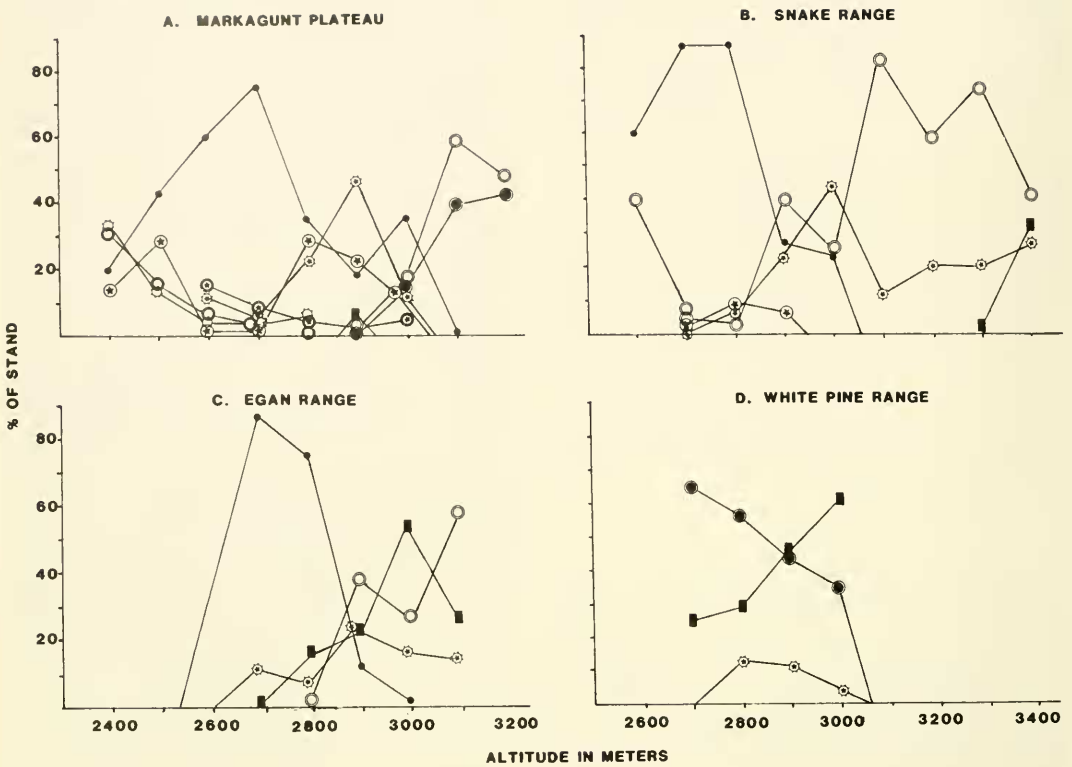


Fig. 2. The relative abundance of montane and subalpine conifers along an altitudinal gradient on the Markagunt Plateau of Utah and three eastern Nevada ranges. Key to species: *Abies concolor* ● (white fir), *A. lasiocarpa* ● (subalpine fir), *Juniperus scopulorum* ○ (Rocky Mountain juniper), *Picea engelmannii* ⊙ (Engelmann spruce), *Picea pungens* ⊕ (blue spruce), *P. flexilis* ⊕ (limber pine), *Pinus longaeva* ■ (bristlecone pine), *P. ponderosa* ⊙ (ponderosa pine), *Pseudotsuga menziesii* ⊕ (Douglas fir).

population boundaries. Individual trees can be found at a wide variety of habitats, however. Stands on the Egan and White Pine Ranges are larger, have a broader altitudinal range, and stand boundaries are less abrupt. Stands here are found to exist on mesic as well as poor edaphic sites.

Estimates of the numbers of individuals per stand and their densities are given in Table 2. Population numbers are high, but densities are low in comparison to more mesophytic conifer stands. Comparisons of densities between populations indicate that WP and WM are similar, but that the density of TF is over twice that of the other two populations. This would appear to be due, at least in part, to the monospecific nature of this population, but may also be due to different physical conditions. Population densities are not

homogeneous among elevation zones (Table 2). Each population has its highest densities at the lower elevations.

Growth rates of individual trees can be used as an indicator of overall environmental hospitality. Beasley (1980) found that bristlecone pine grows best on sites with favorable moisture conditions. However, in these three populations the growth rates of bristlecone pine are low (Table 3). Comparisons among populations indicate that the growth in diameter in WP and TF were effectively equal. On Ward Mountain, however, where bristlecone pine is assumed to be found on a wider variety of sites, mean growth rates are significantly higher ($p < .001$). If growth rates are a good indicator of habitat hospitality, WP has the harshest environment, followed closely by TF.

TABLE 1. Species richness and relative abundances of montane and subalpine conifers on selected ranges in Utah and Nevada.

Species	Relative abundance (%)			
	Markagunt Plateau	Snake Range	Egan Range	White Pine Range
<i>Abies concolor</i>	34	31	40	54
<i>A. lasiocarpa</i>	11	—	—	—
<i>Juniperus scopulorum</i>	5	1	—	—
<i>J. communis</i>	0*	2	1	6
<i>Picea engelmannii</i>	15	34	19	—
<i>P. pungens</i>	4	—	—	—
<i>Pinus flexilis</i>	13	23	16	6
<i>P. longaeva</i>	1	1	24	34
<i>P. ponderosa</i>	5	1	—	—
<i>Pseudotsuga menziesii</i>	12	8	—	—
Total species	10	8	5	4

*Present but less than 1%

Populations TF and WM have similar patterns of individual growth at different elevations within populations, but the pattern in WP differs. Growth rates at the lower elevations of TF and WM are significantly higher ($p < .01$) than those of the middle and upper elevations. This comparison is valid because the growth rates of small and large trees are not significantly different. These results indicate that the lower elevations offer the most hospitable environments.

Tree size (DBH) is often used as an indicator of age. However, since direct estimates of age were obtained from counting growth rings, the size data is not presented. Also, although DBH is significantly correlated ($p < .01$) with age in bristlecone pine, it explains only 70% of the total variation in age. All populations have a mixed size structure with a high proportion of small individuals. This indicates that these forest stands are reproducing themselves (Wikam and Walli 1970).

TABLE 2. Densities (trees/ha) and approximate numbers of individuals of three bristlecone pine (*Pinus longaeva*) populations in Utah and Nevada.

	Twisted Forest (TF)	Wheeler Peak (WP)	Ward Mt. (WM)
Altitudinal zone			
Upper	138	57	51
Middle	138	99	94
Lower	224	75	102
Population mean	163	72	77
Number of individuals	17,000	8,500	14,000

Populations TF and WM have age structures strongly skewed toward the younger age classes. In the absence of any signs of disturbance by man or of any widespread catastrophic events, the age structures suggest an increase in population numbers. The age distribution of WP is indicative of a stationary population. It should be noted that the age structure of WM has certain age classes with few or no trees. This could represent periods of low recruitment or could be an artifact of the sample size. Age classes with few representatives correspond to cool-dry climatic periods at approximately 900 and 2500–3000 years B.P., respectively (LaMarche 1974).

The mean ages of trees in the three elevational zones from population TF are significantly different ($t = 2.274$ to 5.633 ; $p < .01$). The average ages of the high and low ($t = 7.916$; $p < .001$) and the middle and lower portions ($t = 4.218$; $p < .001$) of WM are also significantly different. In contrast, the mean age of trees from the three altitudinal zones within WP were not significant, although the age distributions do not appear to be equivalent.

TF and WM have similar patterns of variation in age structure along the altitudinal gradient. A low proportion of young trees and a high proportion of old trees are observed at the upper elevations, a condition that is indicative of decreasing or stationary population numbers. The intermediate elevations have higher proportions of young trees, but several old trees are also present, in-

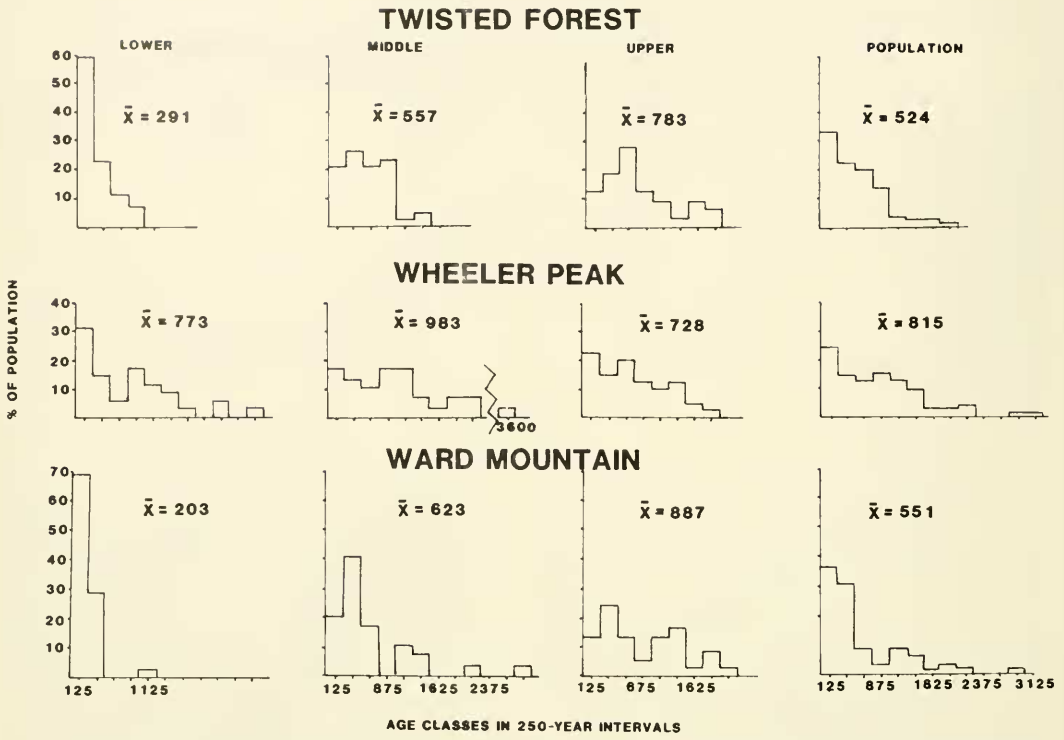


Fig. 3. The age distribution of three *Pinus longaeva* populations in Utah and Nevada. Mean ages and the age distribution at three different altitudes within each population are also given. The age classes are in 250-year intervals.

dicating that population size in the middle zone is either stationary or growing slowly. The presence of many old trees also indicates that bristlecone pine has occupied these areas for some time. The lower portions of these two populations have age distributions strongly skewed toward the younger age classes, with no trees over 1100 years in age.

Population WP does not fit this pattern in all respects, but the age distributions at different altitudes indicate (Fig. 3) that the greatest establishment is presently occurring

at lower elevations. Due to the presence of many old trees, the age distribution at the lower portion of this population is not indicative of a newly colonized site.

The method of Leak and Graber (1974) was applied to the data to test whether bristlecone pine stands are spreading into the lower elevations. This method is based on the premise that population spread is reflected in the relationship of maximum and minimum ages of the trees in the stand. The maximum age should be old and the minimum age

TABLE 3. Average growth rates of trees in DBH in three bristlecone pine (*Pinus longaeva*) populations in Utah and Nevada. Growth rates of trees at different altitudes within populations are also compared. N = the number of trees sampled. Increase in DBH is in mm/yr.

	Twisted Forest	N	Wheeler Peak	N	Ward Mt.	N
Increase in diameter/yr						
Population mean	.864	112	.725	101	1.226	110
Upper	.701	33	.834	37	.963	37
Middle	.645	38	.637	29	1.021	30
Lower	1.200	41	.673	41	1.700	43

*Growth rates of populations or altitude classes connected by lines are not significantly different as determined by the student-t-test. Those not connected are significantly different.

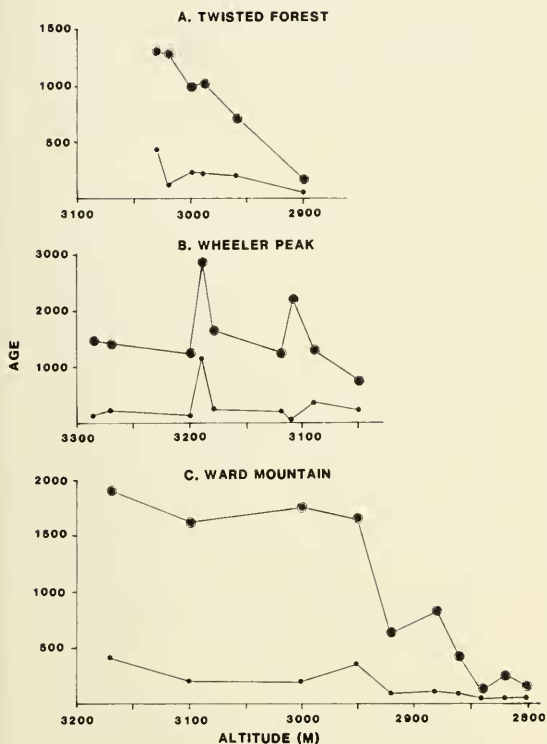


Fig. 4. The age of the oldest and youngest trees along an altitudinal gradient. This method is used to detect migration of forest vegetation (Leak and Graber 1974). Small dots = minimum age. Large dots = maximum age.

young if the population is static in the area. If both the maximum and minimum tree ages are young, the area probably has been recently colonized.

At the higher altitudes of TF (Fig. 4) the maximum and minimum tree ages are old, indicating an old, poorly reproducing stand. The center of this population is static, but the lower portion of the population appears to be recently colonized. The plots (Fig. 4) for WP are not smooth and as a result are harder to interpret. Generally, it appears that the extreme lower portion of the population is a relatively young, newly established stand. Population WM appears to be static at the upper and middle zones, but has only recently become established below 2900 m.

DISCUSSION AND CONCLUSIONS

The distribution of *Pinus longaeva* on these mountain ranges is strongly associated with

species richness of montane and subalpine conifers. Where conifer species richness is relatively high on the Markagunt Plateau and the Snake Range, *P. longaeva* stands are restricted to poor edaphic sites and have abrupt boundaries. On the Egan and White Pine ranges, where conifer species richness is relatively low, the area, altitudinal range, and types of habitats dominated by *P. longaeva* are greatly increased. Why conifer species richness decreases from east to west in the Intermountain Region is subject to debate. It is possible that some conifer species have not had the time or dispersal ability to become established on the middle and western Great Basin ranges (Wells 1983). Alternatively, their ranges may be restricted because environmental conditions are suboptimal or intolerable. The western ranges are more xeric than the eastern ranges due to the rain shadow of the Sierra Nevada of eastern California.

Bristlecone pine is probably absent from the mesic sites (high moisture and nutrient availability) due to its low shade tolerance (Baker 1950). On harsh sites, where it is released from competition for light, it is able to form stands because of its low nutrient and moisture requirements (Beasley and Leemredson 1980). The increased dominance of *P. longaeva* on the Egan and White Pine ranges may result from the suboptimal or intolerable conditions for more mesophytic species such as *Picea engelmannii*. This explanation could be tested by detailed studies of fossil material in woodrat middens dating to the Holocene in the area, coupled with detailed measurements of soil and nutrient levels in the field and testing of relative tolerance ranges for the conifer species involved.

Growth rates of individual trees are slow but highly variable within and among stands, demonstrating the sensitivity of *P. longaeva* to its environment. It is this sensitivity that has made *P. longaeva* so valuable in the reconstruction of past climatic events (LaMarche 1974). The present age structure of these three populations indicates they are maintaining or increasing their numbers. Furthermore, the elevational pattern of age distributions within populations indicates a downward shift in the altitudinal range of *Pinus longaeva* over the last few hundred

years. Obviously, the spatial distribution and abundance of *P. longaeva* on these mountain ranges has varied through time.

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